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DEVELOPMENT, METAMORPHOSIS, AND SEASONAL ABUNDANCE OF EMBRYOS AND LARVAE OF THE ANTARCTIC SEA URCHIN *STERECHINUS NEUMAYERI*

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Abstract

The development to metamorphosis of the shallow-water antarctic sea urchin, *Sterechinus neumayeri,* is described for the first time. Developmental stages are similar to those of closely related temperate species with feeding larvae, but the rate of development is extremely slow. Hatching of ciliated blastulae occurs approximately 140, 128, and 110 hours after fertilization at −1.8, −1.0, and −0.5°C, respectively, more than twice the time required for closely related temperate species near their normal ambient temperature. Larvae reared at −1.8 to −0.9°C are capable of feeding 20 days after fertilization and are competent to metamorphose after 115 days. Early cleavage embryos, blastulae, gastrulae, and prism larvae of this species were collected from the plankton adjacent to McMurdo Station, Antarctica, in early November and December, 1984 and 1985. Echinoplutei were not found during this study, but they have been collected from the plankton in other years; there is no evidence that the larvae are demersal. The timing of spawning ensures that feeding larvae are in the plankton during the abbreviated summer peak of phytoplankton abundance in McMurdo Sound. Recruitment of juveniles into the benthos most likely occurs in synchrony with the subsequent period of high levels of benthic chl *a* concentrations.

Introduction

The perception that brooding is the prevalent mode of development among species of antarctic echinoderms has been firmly established over the past century (Thomson, 1876; Thorson, 1950, Mileikovsky, 1971; Dell, 1972; White, 1984). Brooding is most apparent within the shallow-water echinoid faunas (Arnaud, 1974; Picken, 1980). Three families in three separate orders (Cidaridae, order Cidaroidea; Schizasteridae, order Spatangoida; and Echinidae, order Echinoidea) represent the antarctic echinoids. Two of the three families are dominated by species that brood. Fell (1976) reported that 12 of 19 known species of antarctic cidarids are known brooders, and 3 others almost certainly brood. In addition, females of all 21 known species of antarctic schizasterids brood their young in specialized sunken aboral petaloids known as marsupia (Fell, 1976).

It is unclear whether the high incidence of brooding species among these two families is a consequence of ongoing selection in the antarctic environment or of phylogenetic history (Dell 1972; Fell, 1976; Arnaud, 1977). Fell (1976) hypothesized that the ancestral forms of antarctic cidarids (ancestral goniocidarids) brooded their young, and he suggested that cidarids colonized the antarctic as brooders. No ancestral form has been clearly established for antarctic schizasterids. Since extant non-

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antarctic representatives of this group have unprotected development, the brooding habit of antarctic species may have evolved subsequent to their colonization of the antarctic (Fell, 1976). In either case, the numerical success (*i.e.*, number of species) of cidarids and schizasterids in the antarctic apparently is related—at least in part—to their brooding habits.

In contrast to the cidarids and schizasterids, the antarctic echinids are represented by only five species, all within a single genus, *Sterechinus* (Fell, 1976). Individuals of one species, *S. neumayeri,* are the most abundant echinoids in shallow-water surrounding the antarctic continent. The relatively small maximum egg sizes reported for three antarctic species of *Sterechinus* (0.15 in *S. neumayeri,* and 0.25 mm *S. agassizii* and *S. antarcticus*) are indicative of a free-swimming mode of development (Mortensen, 1909, 1910; Pearse and Giese, 1966). Moreover, despite frequent collections, brooding has not been reported for any of the six species of the genus (Fell, 1976). The absence of post-spawning parental care among antarctic representatives of this group is in sharp contrast with the predominant mode of development in other antarctic echinoids.

Little is known about the embryonic and larval stages of non-brooding antarctic echinoids. Mortensen (1913) described echinoplutei from plankton samples collected by the German South Polar Expedition (1901–1903). Mortensen assigned the larvae to *S. neumayeri* because it was a common species, had very small eggs, and was not known to brood. A pair of echinoplutei was collected from midwater in McMurdo Sound by the British National Antarctic Expedition (MacBride and Simpson, 1908). Mortensen (1913) also assigned these to *S. neumayeri.* Since the publication of these reports over 70 years ago, little additional information on the developmental stages of non-brooding antarctic echinoids has been obtained. Pearse and Giese (1966) described the reproductive cycle of a population of *S. neumayeri* in McMurdo Sound, and suggested that the larvae of this species are demersal and not pelagic because they have been taken from the plankton so rarely; however, the larval development of antarctic echinoids had not been observed or described.

The present paper describes the development through metamorphosis of *Sterechinus neumayeri,* and draws special attention to the slow rates of embryonic and larval development. In addition, we present information on the seasonal abundance of embryos and larvae of this species in the near-shore waters of McMurdo Sound, Antarctica.

Materials and Methods

Individuals of *Sterechinus neumayeri* were collected by scuba divers from 15–25 m depth beneath the annual sea ice adjacent to McMurdo Station, Antarctica (77° 51′ S, 166° 40′ E). In November 1983, immediately after collection, approximately two dozen animals were transported to the University of California, Santa Cruz, where gametes were fertilized and the larvae were reared through metamorphosis in an ice bath (−0.5 to 0.5°C) kept in a 4°C refrigerated unit. Additional studies of the developmental stages and developmental rate of *S. neumayeri* were carried out at McMurdo Station; ripe animals were collected in November, 1984, and larvae were reared through metamorphosis and early juvenile stages to December, 1985. The running seawater system at McMurdo Station maintains aquarium seawater temperatures between −1.8 (winter) and −0.9 (summer)°C, which allowed us to rear embryos and larvae close to their ambient temperatures.

Spawning and fertilization of gametes

Spawning was induced by intracoelomic injection of 0.5 *M* KCl solution. Eggs collected from 3–5 spawning females were washed in clean 5 μm filtered seawater and mixed with a few drops of dilute sperm suspension in a 4 liter polycarbonate culture vessel. After approximately 20 minutes, eggs were filtered off with 20 μm nitex screening and placed in 4 liter culture vessels with clean 5 μm filtered seawater.

Rearing of embryos and larvae

Embryos and larvae were reared in gently stirred and unstirred cultures (Hinegardner, 1969; Strathmann, 1971). The water in the culture vessels was changed every four days using a 20 μm mesh nitex strainer to retain the embryos and larvae.

At McMurdo Station, larvae were fed semi-daily with equal amounts of bacterized cultures of *Isochrysis galbana* and *Phaeodactylum tricornutum* (total concentration 10,000–15,000 cells/ml), which were grown at 15°C in continuous light using half strength F medium (Guillard and Ryther, 1962). Algal samples to be used as food were centrifuged for 10 minutes at 5000 rpm and resuspended in clean filtered seawater (−1.5°C). Phytoplankton concentrations were measured using a Palmer Maloney counting chamber.

Initially, at Santa Cruz, several phytoplankton species (including both temperate and antarctic forms) were tested as potential sources of food for the larvae. Among five temperate species tested (*Amphidinium carteri, Dunaliella tertiolecta, Isochrysis galbana, Phaeodactylum tricornutum* and *Rhodomonas sp.*), *I. galbana* and *P. tricornutum* were most resistant to low temperatures. These phytoplankton appeared to be healthy, even after being in larval cultures for two days, and were readily consumed by the larvae. Cells of the antarctic diatom *Thalassiosira antarctica* were not readily ingested by early stage plutei.

Settlement and metamorphosis of larvae reared in Santa Cruz was induced by adding echinoplutei to glass dishes containing pieces of PVC pipe covered with a bacterial-algal film (Hinegardner and Tuzzi, 1971). The bacterial-algal film was prepared by placing the PVC pipe in a large dish that was held in a running seawater table for several days. Competent echinoplutei reared at McMurdo Station were successfully induced to settle and metamorphose with sediment samples collected from various depths (12, 20, 25, and 30 m) within the adult habitat.

Embryonic developmental rates

Time of development to hatching at different temperatures was determined for embryos reared at McMurdo Station by holding them in culture vials that were (1) in a refrigerated unit at −0.5 (−0.7 to −0.3)°C, (2) in a running seawater table in the laboratory at −1.0 (−1.2 to −0.9)°C, and (3) submerged in the sea 5 m below the level of the sea ice at ambient temperature, −1.8 (−1.9 to −1.7)°C (a small heated hut with a hole in the floor and through the sea ice was used as a staging area). Approximately 50 newly spawned eggs from a pair of females and a single drop of dilute sperm suspension were mixed in each of 3 sets of 10, 5 ml capacity vials filled with 5 μm filtered seawater at the appropriate temperature. Progress of development and incubation temperature were monitored every 12–16 hours during early cleavage stages and every 2 hours near the time of hatching. Because agitation and small changes in temperature may adversely affect rates of embryonic development, only previously undisturbed culture vials were used for observations of developing embryos. The time

of hatching was defined as the time when at least 10% of the ciliated blastulae in a particular incubation vial were released from the fertilization membrane.

Field collection of embryos and larvae

Plankton samples were collected on a weekly or bimonthly basis from September, 1984 to December, 1985 using both diver-towed and stationary current-fed plankton nets (240 μm mesh) at various locations in McMurdo Sound. The conical, stationary nets measured 2 m in length with a circular mouth opening of 0.3 m. The diver-towed net was 2 m long and had a rectangular mouth of 0.1 $\times$ 0.3 m. Each of the current-fed nets was held open continually by a steel frame; net bouyancy was regulated with a float. Two or three nets were attached to a weighted steel cable and suspended by scuba divers from the undersurface of the sea ice for 24 to 48 hours. At the points of attachment to the cable, the nets had a ball bearing swivel which allowed them to orient to the shifting directions of the prevailing currents.

Because the larvae may be demersal, 5 replicate bottom cores of 8 cm diameter were taken monthly from October, 1984 through October, 1985 at 10, 20, 25, and 30 m depth adjacent to McMurdo Station.

All samples were sorted for larvae and other organisms within two days of collection. Early developmental stages that were not readily identifiable were isolated from field samples and reared in the laboratory until they reached a recognizable larval stage. Sizes of embryonic and larval stages as well as larval skeletal morphology of the field-collected specimens were noted and compared to those of embryos and larvae reared in the laboratory from fertilization.

Results

Sequence of development

Development of *Sterechinus neumayeri* was followed through metamorphosis at Santa Cruz (−0.5 to 0.5°C) and McMurdo Station (−1.8 to −0.9°C) (Table I). The eggs are small (mean diameter = 0.179 mm; n = 55) and negatively buoyant. Early development yields a typical sea urchin prism larva. Stomadeal breakthrough occurs 20 days after fertilization at approximately −1.5°C, and soon thereafter the larvae begin to feed. By the 21st day, the postoral and anterolateral paired arms of the echinopluteus are formed. The larval epithelium is now sparsely covered with red pigment granules, more or less randomly distributed. Formation of the posterodorsal and the much shorter preoral pair of arms begins at approximately 43 and 56 days after fertilization, respectively. The onset of the eight-arm pluteus stage is closely timed with the formation of the anterior epaulettes as well as the appearance of the five lobes of the hydrocoel (Fig. 1). At this stage of development the larvae are similar to those previously described from collections of earlier antarctic expeditions (MacBride and Simpson, 1908; Mortensen, 1913).

Further thickening of the ciliary band along the posterior margin of the larva results in the formation of the posterior epaulettes. By approximately the 80th day of development at −1.8 to −0.9°C, the tube feet primordia are formed. Soon thereafter, a variable number (1–3) of triradiate spines appear on the external surface of approximately 40% of the larvae. The most conspicuous of the spines is located in a medial position at the posterior end of the larva, while the other two are formed on the right side, near the bases of the postoral and posterodorsal rods of the larval skeleton.

Metamorphosis is relatively slow, lasting 2–3 hours before the non-feeding benthic juvenile is formed. Newly metamorphosed juveniles retain many of the pigment

TABLE 1

Developmental [illegible] and approximate sizes of developmental stages of Sterechinus neumayeri *reared in Santa Cruz [illegible] (−0.5 to 0.5°C) and McMurdo Station, Antarctica (−1.8 to −0.9°C)*

Developmental stage	Size (mm)	First appearance (days)	
		−1.8 to −0.9°C	−0.5 to 0.5°C
Fertilized egg	.18–.19	—	—
Blastula	.21	2.1	1.7
Hatching	—	5.1	3.7
Gastrula	.22	10	8
Prism	.32	16	15
Early pluteus	.35	21	17
Six-arm pluteus	.54	43	29
Early eight-arm pluteus	.80	56	42
Late eight-arm pluteus	1.20	103	100
Juvenile	.44	115	107

Sizes represent the diameter of ova, blastulae and juveniles, maximum length of gastrulae and prism larvae, and length from the aboral apex to the tips of postoral arms of echinoplutei.

granules characteristic of larval stages, but otherwise have a pale, whitish appearance. They have a single set of well developed tube feet as well as 10 juvenile and 15 primary spines. The triradiate spines which appeared on the surface of echinoplutei are retained on the aboral surface of juveniles.

Duration of embryonic development

Embryos reared below the sea ice (−1.9 to −1.7°C), in a seawater table (−1.2 to −0.9)°C, and in a refrigerator (−0.7 to −0.3°C) at McMurdo hatched at 140, 122, and 110 hours, respectively. Time to first hatching for embryos reared in an ice bath at Santa Cruz (−0.5 to 0.5°C) was approximately 88 hours.

Occurrence of eggs, embryos and larvae in the plankton

One hundred and twenty (120) plankton samples were taken from McMurdo Sound between September, 1984 and December, 1985. Of these, 56 were taken from near the undersurface of the ice or, in the absence of sea ice, near the surface of the water. Fourteen were taken from midwater (10–20 m depth), and 50 were collected from near the bottom at 15–30 m depth.

Large numbers (500–600) of embryos, free-swimming blastulae, and gastrulae that closely resembled those of laboratory reared *Sterechinus neumayeri* were collected from the plankton at all depths sampled using both stationary and diver-held plankton nets. Eggs and early stage embryos were collected predominantly during the third and fourth weeks of November, 1984 and 1985. Hatched blastulae and gastrulae at various stages of development were predominant during the first week of December, although several unhatched and newly hatched blastulae were collected from surface waters on the 9th of November, 1985. Four prism larvae were identified from midwater samples taken in mid to late December, but no echinoplutei were collected during this study. No sea urchin eggs, embryos, or larvae were found in the 240 bottom cores collected and examined.

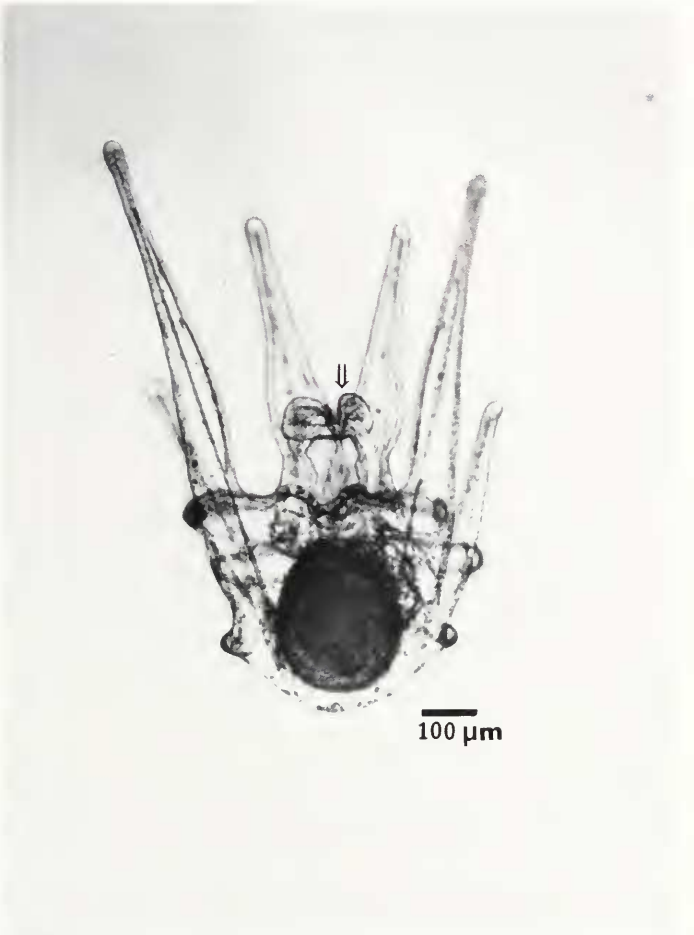

FIGURE 1. Early eight-arm pluteus of *Sterechinus neumayeri* shortly after the formation of the preoral pair of arms (indicated by arrow). Scale bar = 100 µm.

DISCUSSION

Embryonic and larval development

Compared to other species that have been studied, the developmental stages of *Sterechinus neumayeri* are most similar in shape and size to those of the temperate echinoid, *Echinus esculentus* (MacBride, 1903). However, the formation of spines on the external surface of the larvae, separate from the juvenile rudiment, clearly distinguishes the larvae of *S. neumayeri* from those of *E. esculentus* and other species studied within the family Echinidae (MacBride, 1903; Arrau, 1958; Cram, 1971). Morphologically similar spines reportedly develop on the echinoplutei of several other species of regular echinoids, including both euechinoid and cidaroid forms (Onoda, 1931, 1936; Fukushi, 1960; R. Emlet, pers. comm.).

The time of development for the entire period from fertilization to metamorphosis of *Sterechinus neumayeri* is extremely long. Within the family Echinidae, the tem-

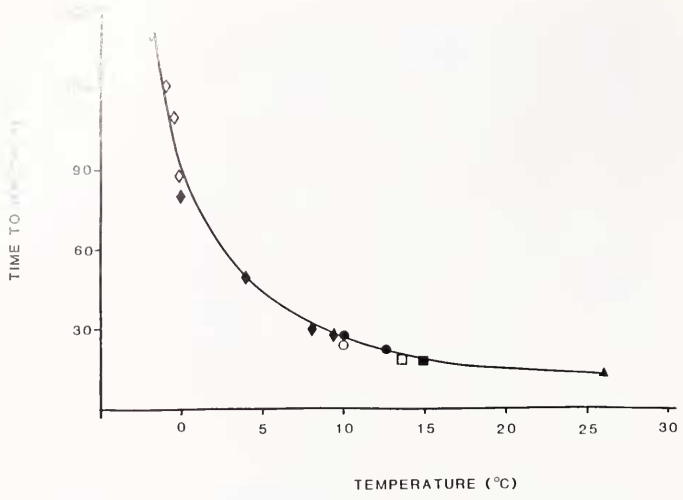

FIGURE 2. Duration of embryonic development to hatching as a function of temperature for seven species of echinids and strongylocentrotids with indirect development. Hatching occurs at the ciliated blastula stage. Mean diameter of ova ranges between 80 (*Strongylocentrotus purpuratus*) to 179 μm (*Sterechinus neumayeri*). ♦ *Strongylocentrotus droebachiensis* reared at 0, 4, 8°C (Stephens, 1980) and 9–10°C (Strathmann, 1974); ● *S. franciscanus* reared at 10, and 12–13°C (Strathmann, 1974); ▲ *S. pulcherrimus* reared at 25–27°C (Onoda, 1936); ○ *S. purpuratus* reared at 10°C (Strathmann, 1974); □ *Loxechinus albus* reared at 13–14°C (Arrau, 1955); ■ *Parechinus angulosus* reared at 15°C (Cram, 1971); ◇ *Sterechinus neumayeri* reared at −1.9 to −1.7, −1.2 to −0.9, −0.7 to −0.3, and −0.5 to 0.5°C (this study).

perate species *Parechinus angulosus* and *Psammechinus miliaris* are competent to metamorphose 60 days after fertilization at ambient temperatures (10–16°C) (Shearer *et al.*, 1913; Cram, 1971), less than half the time required for *S. neumayeri* near their normal ambient temperature (−1.5°C). This observation agrees with the general trend noted by Emlet *et al.* (in press) between decreased temperatures (and increased latitudes) and increased time to metamorphosis for echinoids with planktotrophic larvae.

Because factors unrelated to temperature may influence rates of post-embryonic development (*e.g.*, larval food and density, Kume and Dan, 1968; Hinegardner, 1969), we critically compared the rates of embryonic development to the hatched blastula stage at different temperatures, both of *Sterechinus neumayeri* and other sea urchin species with planktotrophic larvae within the families Echinidae and Strongylocentrotidae. Time to hatching ranged from a minimum of 13 hours at 25–27°C in the tropical species *Strongylocentrotus pulcherrimus* to a maximum of 140 hours at −1.9 to −1.7°C for *S. neumayeri,* and was intermediate for temperate species near their normal ambient temperatures. The duration of embryonic development to hatching for these seven echinoid species is a curvilinear function of temperature, with increased sensitivity at lower temperatures (Fig. 2). A direct relationship between the duration of embryonic development and temperature has been found with interspecific comparisons among other poikilotherm groups, including asteroids (Pearse, 1969), amphipods (Bregazzi, 1972), barnacles (Patel and Crisp, 1960), copepods (McClaren *et al.*, 1969), and rotifers (Herzig, 1983b). Moreover, studies on single species or physiological races reveal the same function, describing the immediate thermodynamic effect of temperature on developmental processes [See for example,

Bougis (1971), Stephens (1972), and McEdward (1985) for temperate echinoids; Herzig (1983a) for copepods; Herzig (1983b) for rotifers; and Ross and Quetin (1986) for antarctic krill]. The direct relationship between temperature and duration of embryonic development, both within a single species and among groups of related species, suggests that there is little or no temperature compensation for developmental rates in poikilotherms, resulting in the observed general trend of increasingly longer periods of development with greater latitude.

The tendency for increased lecithotrophic development among high latitude marine invertebrates was well documented by Thorson (1950) who proposed that the combination of low temperatures—which act to increase development time—and a short season of phytoplankton abundance in high latitude environments select against planktotrophic larvae. Thorson's (1950) explanation has been challenged by several authors. In particular, Underwood (1974) and Clarke (1982, 1983) argue that there should be no *a priori* reason to expect ontological processes to be rate-limited by temperature because all poikilotherms have evolved the capability to modify those processes for the effects of temperature. However, although numerous mechanisms for metabolic temperature compensation have been identified (Hochachka and Somero, 1984), there are few examples of developmental rate compensation for temperature in any previous work (Clarke, 1982). Development is a complex, highly synchronized process involving many biochemical and structural changes. As suggested by Patel and Crisp (1960), basic patterns of temperature-developmental rate interactions may not be readily modified in evolution.

Seasonal abundance and distribution

The presence of embryonic and early larval stages of *Sterechinus neumayeri* in the plankton during early to mid November and December, 1984 and 1985 is in accordance with previous estimates of the spawning time of this species in McMurdo Sound (Pearse and Giese, 1966). Observations of spawning urchins further substantiate this conclusion: males spawned in shallow water near McMurdo Station on two occasions during the first week of November, 1984 (B. Gullikson and T. Klinger, pers. comm.). Coupled with known development times of laboratory-reared embryos and larvae, this evidence suggests that larvae of *S. neumayeri* feed between late December and early March, coinciding with the summer peak of phytoplankton abundance in McMurdo Sound (Bunt, 1964; Rivkin *et al.*, 1986). Consequently, settlement of larvae onto the benthos will occur predominantly during late February and March, in synchrony with the annual period of high benthic chl *a* concentration that occurs during the austral Fall (Berkman *et al.* 1986).

Twenty-five plankton tows and 16 bottom cores were collected and examined between late December and early March, 1984–1985, yet no echinoplutei of *Sterechinus neumayeri* were found. Littlepage (1966, 1968, and pers. comm.) collected and analyzed 547 plankton samples taken throughout the year from McMurdo Sound but found no echinoderm larvae. The conspicuous absence of echinoplutei from plankton samples taken over areas where adult *S. neumayeri* are abundant led Pearse and Giese (1966) to suggest that the embryos and larvae of this sea urchin are demersal. However, large numbers of *S. neumayeri* embryos and early larvae were collected from the water column during this study. Moreover, echinoplutei of this species have been taken from the antarctic plankton in other years: all 48 specimens recorded by MacBride and Simpson (1908) and Mortensen (1913) were taken from the water column; in addition, four echinoplutei of *S. neumayeri* were collected from near-surface waters, over approximately 300 m of water, in early January, 1986 (Rivkin *et*

al., 1986). This demonstrates that embryos and larvae of *S. neumayeri* are readily carried off the bottom by currents. Given the active swimming behavior of echinoplutei in laboratory cultures (I. Bosch, pers. obs.), it is unlikely that development of this species is demersal. More extensive, multi-annual sampling is needed to provide conclusive evidence on the larval distribution of *S. neumayeri*.

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